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Composition and diversity of bat assemblages at Arabuko-Sokoke Forest and the adjacent farmlands, Kenya

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Abstract: Recognized as a global biodiversity hotspot, coastal forests in eastern Africa are currently reduced to fragments amidst human modified habitats. Managing for biodiversity depends on our understanding of how many and which species can persist in these modified areas. Aiming at clarifying how habitat structure changes affect bat assemblage composition and richness, we used ground-level mist nets at Arabuko-Sokoke Forest (ASF) and adjacent farmlands. Habitat structure was assessed using the point-centered quarter (PCQ) method at 210 points per habitat. We captured a total of 24 bat species (ASF: 19, farmlands: 23) and 5217 individuals (ASF: 19.1%, farmlands: 82.9%). Bat diversity was higher at ASF (H′, ASF: 1.48 ± 0.2, farm: 1.33 ± 0.1), but bat richness and abundance were higher in farmlands [Chao1, ASF: 19 (19–25), farmlands: 24 (24–32) species (95% confidence interval [CI])]. Understory vegetation and canopy cover were highest at ASF and the lower bat richness and abundance observed may be the result of the under-sampling of many clutter tolerant and high flying species. Future surveys should combine different methods of capture and acoustic surveys to comprehensively sample bats at ASF. Nonetheless, the rich bat assemblages observed in farmlands around ASF should be valued and landowners encouraged to maintain orchards on their farms.

Keywords: agricultural area; Chiroptera; East Africa; habitat; tropical forest.

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Introduction

Tropical forests cover less than 7% of the Earth's surface but support more than 60% of global biodiversity (Laurance 1999). Human-driven habitat destruction and modification of tropical forests continue to generate human modified habitats that comprise roughly half of the global land surface (Mendenhall et al. 2014). Although considerable biodiversity research has previously been undertaken in the remaining natural areas, managing for biodiversity conservation may ultimately depend on our knowledge of how many and which species cope or even thrive within these human modified habitats. In fact, current research suggests that agricultural areas harbor a large fraction of the world's biodiversity (Johnson et al. 2008, Miller et al. 2009, Dixon 2012).

There is an on-going decline in biodiversity and habitats in Africa (UNEP-WCMC 2016). The coastal forests in eastern Africa and those in the eastern Arc are recognized as a global biodiversity hotspot due to the high level of endemic species (Mittermeier et al. 1998, Myers et al. 2000). Nevertheless, the remaining forest fragments exist as 'islands' in the midst of human modified habitats, mostly farmlands, and are continuously being threatened by a myriad of human activities (Burgess et al. 1998, Burgess and Clarke 2000, Newmark and McNeally 2018). Knowledge on the biodiversity of coastal forest fragments in eastern Africa is poor (Burgess et al. 1998), but even fewer, if any, biological surveys have been done in the agricultural areas around them, and very little is known of their roles in the conservation of biodiversity in this region.

Bats constitute a substantial portion of mammalian diversity in Africa with more than 220 bat species found on this continent (Happold and Happold 2013). Although bats can fly and exploit distant resources in a single night (Treitler et al. 2016), their species richness, abundance and assemblage composition in a given area is influenced by the type of habitat and consequently by habitat degradation (Fenton et al. 1992, Clarke et al. 2005, Peters et al. 2006, Willig et al. 2007, Monroy-Vilchis et al. 2009). For example, the availability and distribution of food-plant species influence the abundance of frugivorous bats (Marciente et al. 2015). The habitat structure, in particular vegetation clutter, seems to

inhibit flight for some bat species (Brigham et al. 1997, Marciente et al. 2015), especially ground foraging bats (Arlettaz 1996, Rainho et al. 2010). This results in lower habitat use and consequently reduced bat activity in thick, cluttered vegetation as compared to more open areas (Humes et al. 1999, Estrada and Coates-Estrada 2002, Law and Chidel 2002, Musila et al. 2018a). However, bat responses to habitat changes are idiosyncratic: abundances of some species may increase, decrease or be unaffected by habitat degradation, loss or fragmentation (Castro-Arellano et al. 2007, Willig et al. 2007, Presley et al. 2008). Although some ecological studies of bat assemblages have been carried out in agricultural areas in Africa (Noer et al. 2012, Taylor et al. 2012, Sirami et al. 2013, Musila et al. 2018a), there is still limited information on how important these habitats may be by complementing bat conservation in natural habitats (Williams-Guillén et al. 2016). There is a need to improve our understanding of bats found in agricultural areas adjacent to forested areas in Africa, in order to understand how to sustainably manage these habitats to conserve bat biodiversity in the continent.

More than 100 bat species occur in Kenya (Patterson and Webala 2012, Musila et al. 2018b), representing almost a third of the mammal fauna of the country (IUCN 2017). Although some studies have documented the biogeography of Kenyan bats (Aggundey and Schlitter 1984, Webala et al. 2004, 2006, 2009, 2014, López-Baucells et al. 2016), only two studies investigated species diversity within protected areas and agricultural landscapes (Webala et al. 2004, Wechuli et al. 2016), and none in Kenyan coastal forests. Managing for biodiversity will depend on our understanding of how many and which species can persist in human modified habitats, particularly in agricultural land. In this context, our main goal was to clarify how habitat structure affects bat assemblage composition and richness, by comparing bat assemblages at Arabuko-Sokoke Forest (ASF) and the adjacent farmlands. In particular, we characterized vegetation structure in the main habitats and assessed species richness, diversity and abundance of the bat assemblages occurring in these habitats. Our ultimate aim was to integrate our results to provide conservation recommendations for biodiversity management in modified human habitats.

Materials and methods

Study area

This study was undertaken at ASF and adjacent agricultural areas. The forest is the largest remaining fragment of coastal forest in eastern Africa, which hosts several endemic and threatened species that are relics of the original diversity of coastal forests (Burgess et al. 1998, Burgess and Clarke 2000). It is located at Gede, along the Kenyan coast, about 100 km north of Mombasa city at a latitude of 3° 20′ S and longitude 39° 50′ E (Bennun and Njoroge 1999). The topography rises from 0 to 135 m above sea level. The mean annual rainfall ranges from 600 to 1100 mm (Muchiri et al. 2001). The weather conditions around ASF include a dry season in January–March, a long rainy season in April–June and a short rainy season in October–December. Temperatures remain high throughout the year with a daily mean of 25°C, and minimal variations monthly, with March usually being the hottest month. Due to the proximity of ASF to the Indian Ocean, humidity is high throughout the year (ASFMP 2002).

The forest has three broad vegetation types: (a) mixed forest comprising relatively dense vegetation covering an area of about 7000 ha with tall and undifferentiated indigenous trees mainly including *Afzelia quanzensis*, *Hymenaea verrucosa*, *Combretum schumannii* and *Manilkara sansibarensis*; (b) *Cynometra* forest thicket, which covers about 23,500 ha which is dominated by *Cynometra webberi*, including *Manilkara sulcata*, *Oldfieldia somalensis* and few *Brachylaena huillensis* and (c) *Brachystegia* forest which covers about 7636 ha and is dominated by *Brachystegia spiciformis* (Muriithi and Kenyon 2002, Figure 1). The forest is an internationally recognized biodiversity hotspot (Oyugi et al. 2007). Although the ASF is legally protected, it is an 'island' in the midst of a densely populated area, with most of the areas around it modified into agricultural areas and human settlements (ASFMP 2002, Oyugi et al. 2007, Habel et al. 2017).

The agricultural areas surveyed, here collectively referred to as 'farmlands', occur on the eastern part of ASF at Mtsangoni, Mkangani, Mida, Arabuko, Gede, Watamu and Msabaha villages (Figure 1). Most of the farmland area was dominated by agriculture and human settlements. The main tree species found in these farms were mango (*Mangifera indica*), cashew nut (*Anacardium occidentale*), neem (*Azadirachta indica*) and coconut (*Cocos nucifera*). Other trees occasionally found in the farms were Indian almond (*Terminalia catappa*), casuarina (*Casaurina equesitifolia*), guava (*Psidium guajava*), sugar-apple (*Annona squamosa*) and gamhar (*Gmelina arborea*) (Musila et al. 2018a,c). The mango, cashew nut, guava and neem trees in the farmlands produce fruits, which when ripe are eaten by fruit bats (Ayensu 1974, Happold and Happold 2013, Aziz et al. 2016). Coconut and mango trees were the most abundant trees in some farms, while others had a mixture of these and other trees. Sampling stations

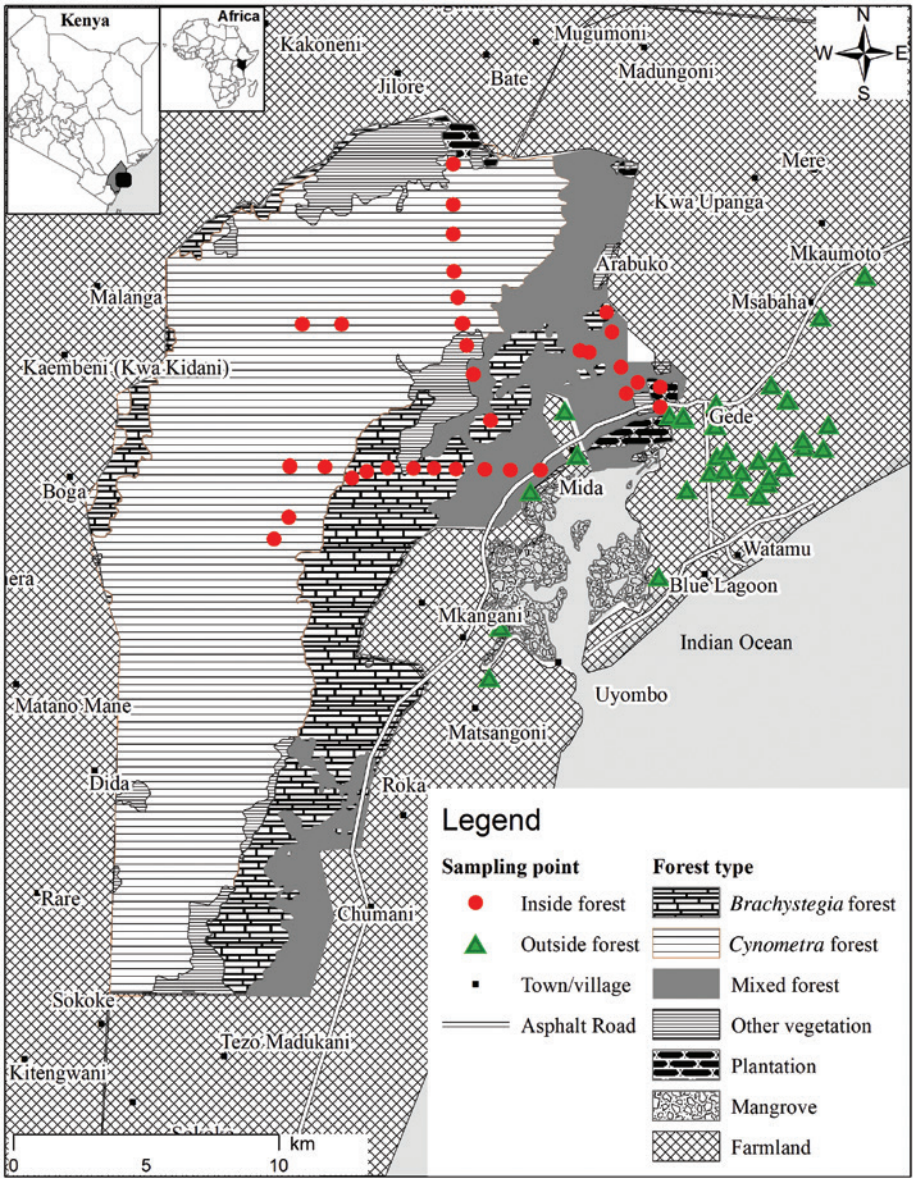

Figure 1: Map of Arabuko-Sokoke Forest (ASF) in Gede, Malindi-Kenya, including the different vegetation types in the forest interior (sampled sites in red dots) and villages sampled within farmlands (sampled sites in green pyramids) around the forest (Musila et al. 2018a).

were thus visually classified as mango farms (MAN) and coconut farms (COC) when one of these two species were the most abundant in the site, and as mixed farms (MixFa) when other trees species dominated. Some farms were left fallow and growing with the above-mentioned trees or some sections of the farms were cultivated with maize, beans, cowpeas, some pawpaw and cassava. Most of the farms had man-made structures that could potentially be used by bats for roosting (Voigt et al. 2016, López-Baucells et al. 2017). Some large limestone caves with large bat populations of multiple species (Musila et al. 2018c) also existed in the farmlands. The mango, cashew nut, coconut and neem trees are evergreen species; hence, their well-sheltered tree crowns and foliage could also be used by bats for roosting (Ayensu 1974, Happold and Happold 2013). Sampling was performed only where permission was granted by land owners or guardians.

Habitat structure assessments

The point-centered quarter (PCQ) method was used to sample vegetation in all sites (Cottam and Curtis 1956). The PCQ is a method of sampling forest communities

which uses a set of random points usually positioned along a transect line traversing an area of interest (Cottam et al. 1953). At ASF, transects used to identify PCQ points were laid following roads in the general areas used to sample bats within *Cynometra*, *Brachystegia* and mixed forests. In the farmlands, transects were laid following the longest orientation of the MAN, COC or MixFa, to maximize on the number of points that could be sampled in one farm, as the sizes of some of the farms we sampled bats were very small (4 ha). The starting point for vegetation survey at ASF was a random point which was 200 m from the edge of a different vegetation type, while in the farmlands it was 30 m from the boundary with edge of the nearest farm. PCQ points were selected along a transect, at an interval of 30 m away from each other in order to ensure that same trees were not sampled in two different points. In each quarter, we recorded the nearest tree species of at least 20 cm diameter at breast height (DBH) measured by a ruler, with the distance of the tree from the center of PCQ point estimated by pacing (Mitchell 2007). We avoided smaller trees (<19 cm) due to potential size differences in providing shelter to bats (Ragusa-Netto and Santos 2014), mainly because bigger trees are more likely to be used as foliage or hollow roosts by bats (Fenton and Rautenbach 1986, Taylor and Savva 1988, Smith et al. 2008). We sampled farms cultivated with different fruit trees in the farmlands, because the seasonal changes in fruit production, as well as tree sizes (DBH and crown configuration), might influence their exploitation by foraging and roosting bats of different species. A total of 70 PCQ points were assessed in each of the six vegetation types sampled in each habitat. We used cover boards to assess the percentage understory vegetation thickness (Robel et al. 1970, Nudds 1977). A plywood board, painted in white-and-red checkerboard pattern (twenty-five 10×10 cm squares), was used to assess the percentage understory vegetation cover around each PCQ point. One observer counted the number of squares that were >50% obscured by vegetation from a board held at 1.5 m above the ground at a distant of 5 m from the centre of PCQ point in the north and south compass directions. The percent canopy cover was assessed by eye (Korhonen et al. 2006, Lentini et al. 2012) using a toilet paper roll as a sighting tube, by estimating the percentage vegetation directly above which covered the exposed area (45 mm in diameter, 98 mm long) of the toilet tube (Fanshawe 1993). The sighting tube was always held vertically at each point to reduce the error in percent canopy cover estimation (Jennings et al. 1999). Count of squares, canopy and understory cover assessments were made by the same observer throughout to control for observer bias.

Bat surveys

Bats were sampled in six vegetation types: three at ASF (*Cynometra*, *Brachystegia* and mixed forests) and three on the farmlands (MAN, COC and MixFa). A total of 81 sites were sampled in each habitat type, including 27 mist-netting stations in each of the three vegetation types in each habitat, in November, February and June between 2014 and 2016 (Table 1). Ground-level mist nets (12 m long by 2.5 m wide, 16-mm mesh, four shelves, Ecotone, Gdynia, Poland) were used to capture bats. ASF and farmlands were sampled alternatively, one day in the forest and the next in farmlands, to reduce the decrease in bat captures by repeated sampling in the same site (Simmons and Voss 1998, Castro-Arellano et al. 2007, Kunz et al. 2009, Marques et al. 2013).

Table 1: Number of bat surveys, sampling seasons and stations surveyed, hours and sampling efforts at ASF and in farmlands.

Survey month	Season	Survey hours (start–end)	Surveyed hours/ night (A)	Nets (m)/ habitat (B)	No. of mist nets/ station (C)	No. of nights – ASF (D)	No. of nights – farmlands (D)	Total sampling effort – ASF	Total sampling effort – farmlands
Nov-2014	Short rain	19–24	5	12	5	9	9	2700	2700
Feb-2015	Dry	19–01	6	12	5	12	12	4320	4320
Jun-2015	Long rain	19–01	6	12	5	12	12	4320	4320
Nov-2015	Short rain	19–05	10	12	5	12	12	7200	7200
Feb-2016	Dry	19–05	10	12	5	12	12	7200	7200
Jun-2016	Long rain	19–05	10	12	5	12	12	7200	7200
Nov-2016	Short rain	19–23	4	18	2	12	12	1728	1728
Total						81	81	34,668	34,668

Total sampling effort (net meter hour) in each habitat per season was calculated by multiplication of the total hours surveyed per night (A), the length (B) and the number of nets (C) used per habitat (B) and the number of nights surveyed per habitat (A*B*C*D).

Nets were checked every 15 min within the first 2 h, and thereafter after 30 min the rest of the night. The nets were always opened at 19 h, and closed at varying time in different sampling months each year. Nonetheless the total number of sampling hours, bat mist-netting stations and the length of mist nets used in each vegetation type at ASF and in farmlands in each month and year were always the same (Table 1).

Mist nets were erected at least 100 m apart (Harvey et al. 2006), with the sampling stations in each vegetation type being at least 1.5 km from each other to minimize pseudoreplication. In the forest, nets were erected diagonally across existing roads which potentially act as bat flyways. In the farmlands, nets were erected in the gaps between two trees or row of trees, or in the open areas under tall trunked coconut trees. Captured bats were kept singly in large cotton bags and released at each sampling station. Due to the large number of bat species occurring in the region and the complexity associated with the identification of most of them (Patterson and Webala 2012), two individuals were collected as voucher for each bat species, preserved in 70% ethanol (Supplementary Appendix 1). After validation of the identification made in the field, each voucher specimen was deposited in the Mammalogy Section of the National Museums of Kenya (NMK). Bats were identified by comparison with specimens preserved at NMK as well as using keys published in Monadjem et al. (2010), Patterson and Webala (2012) and Mammals of Africa (Happold and Happold 2013). Our field protocol followed the guidelines recommended by the American Society of Mammalogists (Sikes and Gannon 2011). For taxonomy and common names of bats, we follow Happold and Happold (2013). Permission to work and collect vouchers at ASF and its immediate environment was provided by Kenya Forest Service (KFS) (RESEA/1/KFS) VOL. IV/71 and NMK (NMK/ZLG/LEG/3).

Data analyses

To compare the habitat structure variables obtained in this study, and after checking for normality and variance homogeneity, a multivariate analysis of variance was performed, followed (if p-value <0.05) by Tukey's honestly significant difference test. This analysis was performed using the mulcomp package in the R environment (v.3.5.1; The R Foundation for Statistical Computing, Vienna, Austria). The total bat sampling effort was estimated using the method described by Medellín (1993) as the product of length of all nets in meters multiplied by the total hours worked (net meter hour = nmh), which also allows for the estimation of relative abundance of a species by dividing the number of captured bats by sampling effort. We used the program EstimateS 9.1.0 to build rarefaction curves, which are useful tools for comparing abundance and diversity between habitats and to estimate total bat species richness for forest and farmlands, using two non-parametric estimators: Chao1 and Jacknife1 (Heltshe and Forrester 1983, Chao 1987, Colwell et al. 2012). Diversity was estimated using the exponential of the Renyi index (Tóthmérész 1995) which depends on the value of α; for $\alpha = 1$, this index will be equivalent to the Shannon-Wiener index (Shannon and Weaver 1963), while $\alpha = 2$ will estimate an index that behaves like the Simpson index. Morisita similarity (Morisita 1959) was used to compare bat species composition between farmlands and forest interior. Unweighted pair group method with arithmetic (UPGMA) dendrograms, with Ward's method, Euclidean distances and 40 bootstraps used to define the branching measurements, were used for classifying the similarity of bat assemblages among vegetation types in terms of composition and abundance of the various bat species. The cophenetic correlation coefficient was used as a measure of goodness of fit of the dendrogram, assessing how faithfully it preserves the original Euclidean distances between points. Correspondence analysis which provides the ordination of species and vegetation types was performed to aid the understanding of how bat assemblages are organized. The UPGMA dendrograms, correspondence analysis and diversity indices were computed using the program PAST 3.16 (PAleontological Statistics; Hammer et al. 2001).

Results

Habitat structure at ASF and in farmlands

Overall, in the farmlands, the most common tree was *Cocos nucifera* (54%), followed by *Mangifera indica* (31%). The most abundant trees in 70 PCQ points sampled in each vegetation type in the farmlands were: in MAN *M. indica* (71%), in COC *C. nucifera* (89%) and in MixFa *C. nucifera* (53%), *Anacardium occidentale* (23%) and *M. indica* (19%). Overall, at ASF, the most common tree was *Brachystegia spiciformis* (30%), followed by *Cynometra webberi* (29%) and *Manilkara sansibarensis* (18%). The most dominant trees in the sampled 70 PCQ points in each vegetation type at ASF were: in *Brachystegia* forest *B. spiciformis* (87%), in mixed forest *M. sansibarensis* (54%)

and in *Cynometra* forest *C. webberi* (87%). Most of the individuals of *M. sansibarensis*, *Markhamia obtusifolia* and *Dialium orientale* were recorded in the mixed forest. Habitat characteristics, both at ASF and in farmlands, significantly vary between vegetation types (Figure 2), with the most striking difference being the understory

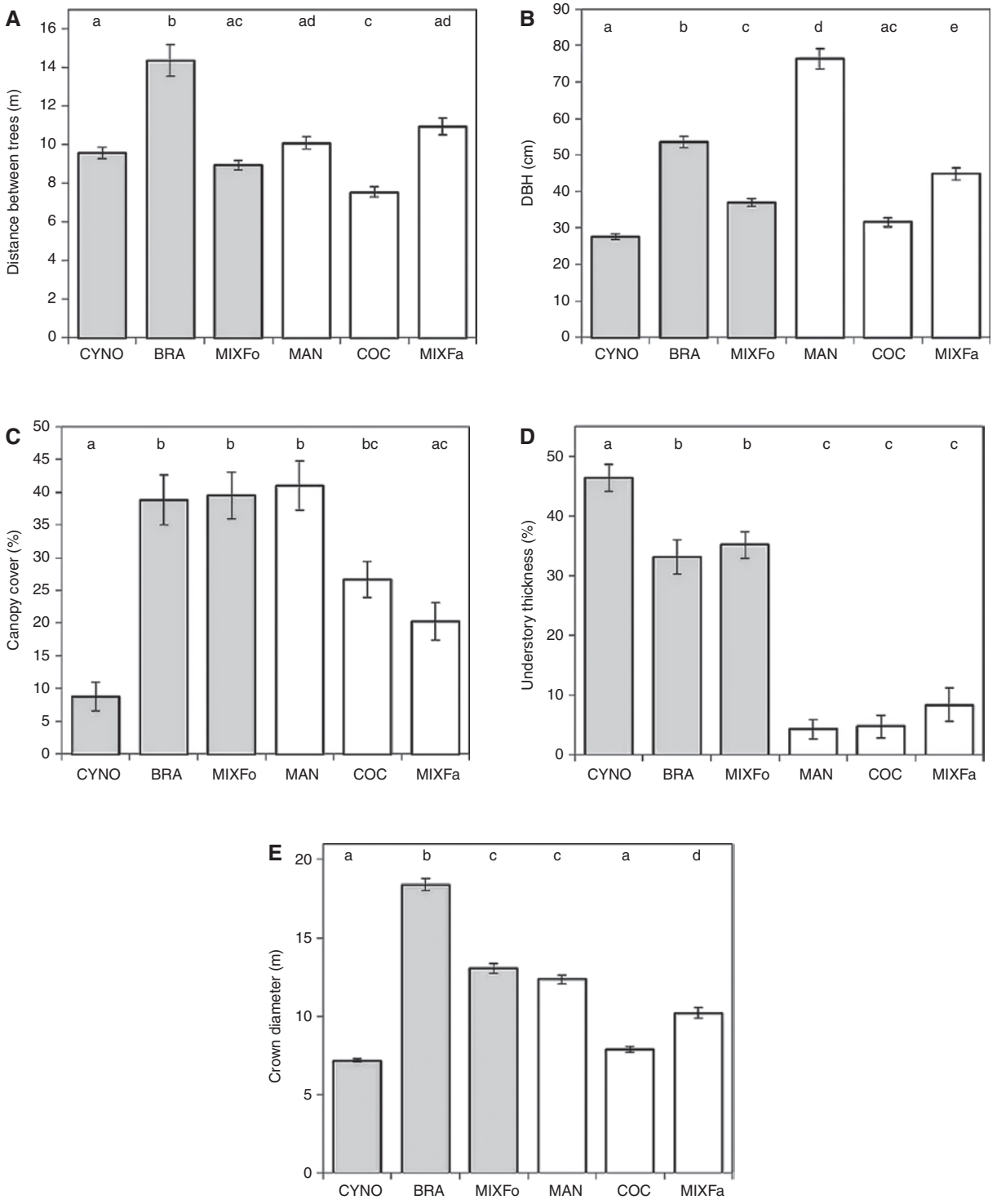

Figure 2: Mean values (±SD) of distance between trees, diameter at breast height (DBH), canopy cover, understory thickness and crown diameter at different vegetation types considered.
ASF vegetation types are shaded. The different letters indicate significant differences at $p = 0.01$. Sample size of 280 for all variables except canopy cover and understory thickness, with a sample size of 70.

thickness ($F = 61.56$, $p < 0.001$) which was much higher in all ASF vegetation types (Figure 2D). The *Cynometra* forest, compared to the other vegetation types at ASF, had much lower canopy cover (Figure 2C) and crown diameter (Figure 2E) but significantly higher understory thickness (Figure 2D).

Bat assemblage composition and species abundance

A total of 5217 bats was captured during this study, 82.9% of which were captured in farmlands and 19.1% at ASF (Table 2). Mixed forest at ASF had the largest number of

Table 2: Total bat captures per site and per species, species richness, abundance and diversity in the different vegetation types at ASF [*Cynometra* forest (CYN) *Brachystegia* forest (BRA), mixed forest at ASF (MIXFo)] and in farmlands [mango farms (MAN), coconut farms (COC) and mixed farms (MIXFa)].

Survey sites	IUCN status	Arabuko-Sokoke Forest			ASF	Farmlands			Farmlands
Vegetation types	2018	CYN	BRA	MIXFo	Total	MAN	COC	MIXFa	Total
Pteropodidae									
1. *Rousettus aegyptiacus* (É. Geoffroy, 1810)	LC	27	59	228	314	888	744	727	2359
2. *Epomophorus wahlbergi* (Sundevall, 1846)	LC	206	59	153	418	400	271	363	1034
3. *Eidolon helvum* (Kerr, 1792)	NT			1	1	4			4
Rhinolophidae									
4. *Rhinolophus deckenii* Peters, 1868	NT	8	1	1	10	10	5	15	30
Hipposideridae									
5. *Hipposideros caffer* (Sundevall, 1846)	LC	13			13	2	8	13	23
6. *Macronycteris vittata* (Peters, 1852)	NT	7	6	7	20	17	11	14	42
Rhinonycteridae									
7. *Triaenops afer* Dobson, 1871	LC					1	4		5
Megadermatidae									
8. *Cardioderma cor* (Peters, 1872)	LC		2		2	146	215	260	621
Emballonuridae									
9. *Coleura afra* (Peters, 1852)	LC	1	10	6	17	1	3	19	23
10. *Taphozous mauritianus* É. Geoffroy, 1818	LC	1			1	5	2		7
Nycteridae									
11. *Nycteris thebaica* É. Geoffroy, 1818	LC	1	13		14	6	12	22	40
Molossidae									
12. *Chaerephon pumilus* (Cretzschmar, 1826)	LC	3			3	2			2
13. *Otomops harrisoni* Ralph, Richards, Taylor, Napier & Lamb, 2015	VU						10	1	11
Miniopteridae									
14. *Miniopterus minor* Peters, 1867	DD	14		5	19	2	10	3	15
15. *Miniopterus cf inflatus* Thomas, 1903	LC	1	1		1	1			1
Vespertilionidae									
16. *Mimetillus moloneyi* (Thomas, 1891)	LC			3	3				
17 *Neoromicia capensis* (A. Smith, 1829)	LC	2	3		5	3	1	2	6
18. *Neoromicia nana* (Peters, 1852)	LC	15	4		19	10		2	12
19. *Neoromicia rendalli* (Thomas, 1889)	LC						1		1
20. *Neoromicia tenuipinnis* (Peters, 1872)	LC						5	1	6
21. *Nycticeinops schlieffeni* (Peters, 1859)	LC	1	4	8	13	13	1	6	20
22. *Pipistrellus rueppellii* (Fischer, 1829)	LC	5			5		3	1	4
23. *Scotoecus hirundo* (de Winton, 1899)	LC						8	2	10
24. *Scotophilus trujilloi* Brooks & Bickham, 2014	LC	1	3	7	11	16	30	5	51
No. of species		16	12	10	19	18	19	17	23
No. of insectivorous bats		73	47	37	157	239	329	366	930
No. of fruit bats		233	118	382	733	1288	1015	1090	3397
No. of bat individuals		306	165	419	890	1527	1344	1456	4327
Trap stations/vegetation type		27	27	27	81	27	27	27	81
Net meter hours (NMH)		11,556	11,556	11,556	34,668	11,556	11,556	11,556	34,668
Bats/NMH		0.03	0.01	0.04	0.03	0.13	0.12	0.13	0.12

captured bats (419), while in the farmlands it was in MAN (1527). Of 5217 captured, 79% were fruit bats and 21% were insectivorous bats. *Rousettus aegyptiacus* and *Epomophorus wahlbergi* were the most common species, both at ASF and in farmlands, accounting for 78% of all bats captured in farmlands and 52.4% in forests. The only other frugivorous species recorded in the study area was *Eidolon helvum* with only five individuals captured. The largest number of fruit bats was captured in mixed forest at ASF (381), while in the farmlands it was in MAN (1288). The number of captured insectivorous bats was generally much lower both at ASF and in farmlands. An exception was *Cardioderma cor* with 621 individuals captured in farmlands, but only two individuals at ASF (Table 2). At ASF, the largest number of insectivorous bats was recorded in *Cynometra* forest (73) while in the farmlands it was in mixed vegetation farms (366).

The UPGMA dendrogram has a good adjustment to the original data (cophen. correl. = 0.959, Figure 3), and shows that species' composition and abundance are quite dissimilar in the two main habitats as it clearly separates the ASF and farmland vegetation types. The correspondence analysis (Figure 4) which maximizes the degree to which (a) sites with the most similar species assemblages and (b) species that have comparable habitat use, are adjacent in the graph, corroborates this pattern. It shows the three farmland vegetation types in a cluster close to the center of the graph axis – associated with abundant bat species like *Cardioderma cor* and *Rousettus aegyptiacus*. Bat assemblages in the three ASF vegetation types seem to be more different, with mixed forest showing a closer similarity to farmlands and *Cynometra* forest proving to host the most distinct bat assemblage.

Bat species richness and diversity

A total of 24 bat species were recorded in this study including 19 at ASF and 23 in farmlands (Table 2). Eighteen species were shared between ASF and farmlands resulting in a Morista similarity of 65.8%. Five species were exclusively recorded in the farmlands and three individuals of *Mimetillus moloneyi* only within ASF (Table 2). At ASF, the largest number of bat species was recorded in *Cynometra* forest (16), while in the farmlands it was in COC (19). The site-based rarefaction curves confirmed a reasonable mist-net sampling effort in both habitats (Figure 5) and showed a significantly lower estimated species richness at ASF than in farmlands. Other richness estimators confirmed this pattern, including the Jacknife1 that estimated 23 [±1.9 standard deviation (SD)] at ASF and 26 (±1.3) in farmlands and Chao1 that estimated 19 [95% confidence interval (CI) 19.0–25.0] species at ASF and 24 (24.0–32.3) species in farmlands. The bat assemblage in farmlands had some overly abundant species (Table 2), making evenness significantly higher in forested habitats (forest: 0.48 ± 0.1, farmlands: 0.22 ± 0.05). Both indices suggest a higher diversity at ASF (ASF: Shannon $H' = 1.48 \pm 0.2$, Simpson 1-D = 0.65 ± 0.02; farmlands: $H' = 1.33 \pm 0.1$, 1-D = 0.62 ± 0.01). This result should

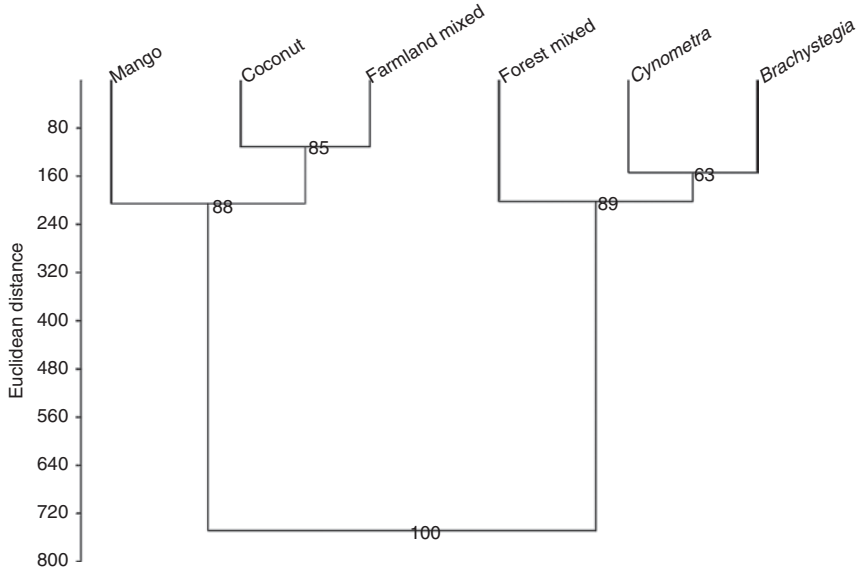

Figure 3: UPGMA dendrogram (using Euclidean similarity index) on the dissimilarity among studied vegetation types in terms of abundance of the various bat species.

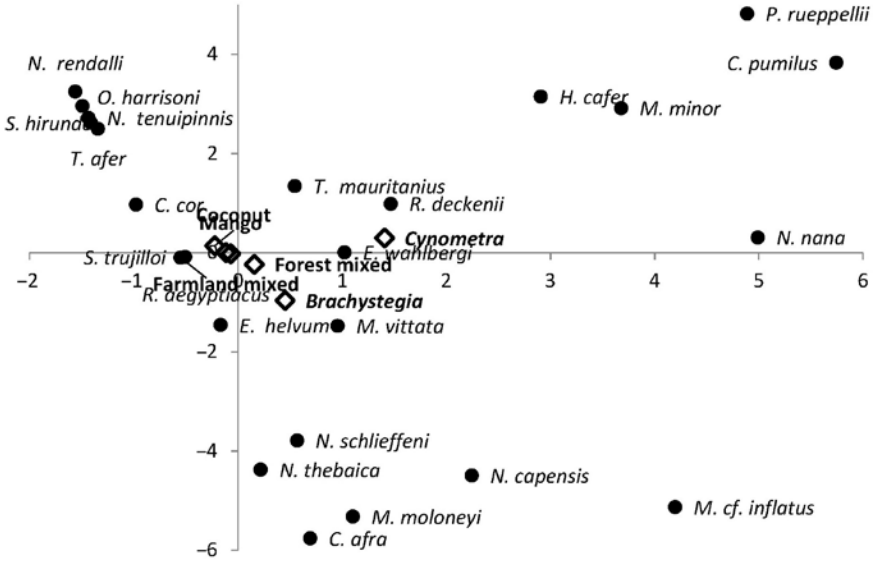

Figure 4: Correspondence analysis of studied vegetation types (open diamonds) and species (black dots) using bat species abundance.

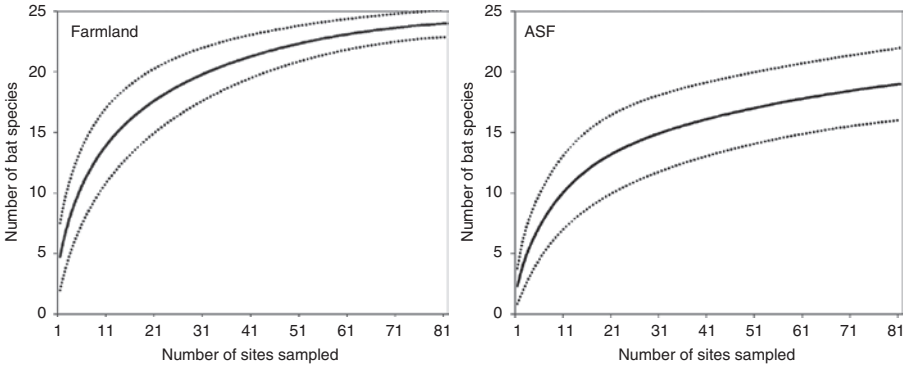

Figure 5: Sample-based rarefaction curves using Chao1 estimator for bat richness at Arabuko-Sokoke Forest (ASF) (left) and surrounding farmlands (right), showing the expected species richness values (solid lines) and 95% confidence intervals (dashed lines) in each of these habitat types.
The significantly higher species richness estimated for farmlands is confirmed by the non-overlapping confidence intervals of both curves.

however be interpreted with some care, as the diversity profiles of both habitats cross due to the higher species richness observed in farmlands, rendering the diversities non-comparable (Tóthmérész 1995).

Discussion

ASF is the largest continuous coastal forest in East Africa, which is dominated by indigenous trees and shrubs. However, its surroundings is completely modified into agricultural areas and other human infrastructure. Our results showed that the wooded areas within farmlands were mostly orchards of a limited set of exotic cultivated fruit trees. These trees bring direct benefits to farmers and therefore the sampled trees (of DBH 20 cm) were densely planted (mean distance 9.5 m ± 5.95 m from each other). Probably to maximize fruit productivity and allow for cultivation of other food crops, the undergrowth of orchards was cleared to facilitate access and perhaps reduce competition for water and nutrients (Atay et al. 2017). The orchard trees were probably cultivated for many years, and often mango trees attained very large girths (mean of 76 cm) and crown diameter (12 cm). ASF had a completely different habitat structure; with a very high secondary growth, vegetation was dense and cluttered near the ground (< 3 m). Bat assemblages also proved to be different between these two habitats. Bat assemblages in farmlands were richer with some species being overly abundant. Nevertheless,

species evenness and diversity was higher within the forested habitats. The observed bat diversity in the interior of ASF (H′ = 1.44) was slightly lower than that observed by Cockle et al. (1998) in smaller patches of coastal forest in Tanzania (H′ = 1.55–1.97) and far lower than that observed by Wechuli et al. (2016) in *Acacia* woodlands in Kenya (H′ = 2.96). The differences in bat diversities in these study sites may be as a result of variations in vegetation types, habitat structure, food and/or roost availability.

The differences observed in the habitat structure of the vegetation site studies are reflected in the UPGMA dendrogram and in the correspondence analysis (Figures 3 and 4) that clearly show the dissimilarity of the bat assemblages occurring in the main habitats. Striking is also the higher dissimilarity of the bat assemblage occurring in the *Cynometra* forest, generally associated with a higher richness of insectivorous bat species, as the habitat structure of this vegetation type was also very different from the remaining types (Figure 2C–E). Overall, our results indicate higher bat abundance and species richness in the farmlands, although diversity was highest at ASF. These results contrast with those of Webala et al. (2004) and Wechuli et al. (2016), who recorded lower bat species richness and abundance in farmlands around Meru National Park and Bogoria National Reserve, respectively. A number of hypotheses (not mutually exclusive) could explain these contrasting results.

Limitation of mist nets in bat surveys

Our results may not represent a comprehensive bat species richness especially at ASF. This is because not one single method of sampling bats can capture all bat species at study site (Sampaio et al. 2003, MacSwiney et al. 2007), and mist nets provide a biased sample of insectivorous and echolocating bat species assemblages (Murray et al. 1999, Ratcliffe et al. 2005). Hence, the lower species richness and abundance at ASF may be a result of sampling bias associated with ground-level mist netting. Forest interior bats also referred to as clutter tolerant species such as rhinolophids, nycterids, some hipposiderids and vespertilionids are skillful at detecting and avoiding mist nets (Kunz et al. 1996, Lang et al. 2004, MacSwiney et al. 2008). Also, higher fliers like mollossids and emballonurids were also not represented because they fly high above the forest canopy beyond the reach of ground-level mist nets (Kunz and Kurta 1988, Simmons and Voss, 1998, Meyer et al. 2011). It is also possible that the five bat species (*Triaenops afer, Otomops harrisoni, Scotoecus hirundo, Neoromicia rendalli* and *Neoromicia tenuipinnis*) exclusively recorded in farmlands might also occur at ASF, but were missed due to above-mentioned sampling bias. Furthermore, other bat species like *Rhinolophus fumigatus*, *Doryrhina cyclops*, *Macronycteris gigas*, *Cloeotis percivali*, *Taphozous hildegardeae*, *Taphozous perforatus*, *Mops brachypterus*, *Mops condylurus* and *Scotophilus nigrita* occur along the Kenyan coast (Happold and Happold 2013), but we missed them in our surveys. Further surveys will be necessary using complementary bat sampling methods such as canopy nets and acoustics (Barclay 1999, O'Farrell and Gannon 1999, Flaquer et al. 2007, Larsen et al. 2007), in order to produce a more comprehensive inventory of bats at ASF as well in the farmlands.

Differences in vegetation structure may affect bat habitat use and capture success

The understory vegetation at ASF was about 7 times thicker than that in farmlands, while the percentage of canopy cover at ASF (42.8%) was generally more closed than that in farmlands (29.3%). Vegetation structural heterogeneity may play an important role in determining the composition, abundance and micro-habitat use of bat assemblages within forested areas (Adams et al. 2009). Bats are known to display vertical stratification and exploit the tridimensional space differently depending on vegetation structure (Ramos-Pereira et al. 2010, Marques et al. 2016). Within forested habitats some bat species may use the tree canopy more often than the space near the ground, while in the farmlands with many open spaces other bat species will fly near the ground and be easier to capture (Simmons and Stein 1980, Neuweiler 1984, Barclay 1985, Aldridge and Rautenbach 1987, Menzel et al. 2005). This probably may explain the large number of insectivorous bats captured in farmlands (930) as compared to very few at ASF (157). Hence, ground-based studies, like this one, underestimate the survey of bat species flying at or above the tree canopy and are unlikely to assess the spatial distribution of bats, particularly in the more complex and heterogeneous forested areas. In addition, at the ground level, vegetation clutter may also exert a strong influence on bat abundance and species composition (Bobrowiec et al. 2014, Marciente et al. 2015), as it can inhibit flight for some species (Brigham et al. 1997) and make prey location and capture more difficult (Rainho et al. 2010, Müller et al. 2012). Additionally, bats adjust their flight and echolocation when flying in cluttered environments (Falk et al. 2014) making it probably easier for bats to detect and avoid mist nets while flying within the ASF. Fruit bats may also avoid dense forested habitat because of their large

wingspan and limited ability to maneuver across many obstacles in search of fruits. This again may explain the lower number of individuals of fruit bats captured at ASF, compared to more open farmlands which facilitated flight and easier exploitation by foraging and/or commuting bats.

Large fruit availability in farmlands and capture of fruit bats

About 65% of all bats recorded in this study were fruit bats found in the farmlands. Fruit bats are easily captured in mist nets, because they do not echolocate (except *Rousettus aegyptiacus*), often depend on their sight to find direction and thus have limited ability to detect and avoid mist nets (Fleming and Robinson 1987, Desvars et al. 2009). This probably explains the large number of fruit bats captured in farmlands. Another factor that may explain fruit bat abundance in farmlands is the large quantities of cultivated fruit trees. Forty-six percent of trees found in the farmlands including mangos, cashew nuts, neem, guavas, sugar-apples and gamhar trees would produce fruits targeted by fruit bats. Frugivorous bats have been observed to be more abundant in disturbed sites that provide fruit and nectar on which these bats feed. For example, higher fruit bat abundance was found in farmed areas than forest areas, in the Neotropics (Clarke et al. 2005, Castro-Arellano et al. 2007, Presley et al. 2008), Asia (Fukuda et al. 2009, Heer et al. 2015) and in the Pacific Islands (Luskin 2010). Individual species like *R. aegyptiacus* and *Epomophorus wahlbergi* feed not only on ripe fruits of many native trees and shrubs but also on ripe cultivated fruits (Korine et al. 1994, Happold and Happold 2013). The higher availability of fruiting trees in the farmlands is the most plausible explanation for the large numbers of fruit bats recorded in these habitats. In the farmlands, the largest number of fruit bats was recorded in MAN (1288), suggesting that fruit bats may select this habitat for foraging ahead of others due to the likelihood of encountering some ripe fruits. Within the forest, the largest capture of fruit bats was in the mixed forest, which had high abundance of *Manilkara sansibarensis*, *Markhamia obtusifolia* and *D. orientale*, trees that produce small edible fruits with soft fruit pulp when ripe (Beentje 1994), which are likely to be eaten by fruit bats.

In conclusion, even though the farmlands were richer in species and abundance of both insectivorous and frugivorous bats than at ASF in our study, these results should be interpreted with caution. Ground-level nets underestimate the capture of bats flying above the tree canopy and those skillful at mist-net detection. Hence, future bat surveys should employ a combination of methods, high canopy nets and acoustic surveys, to provide a more comprehensive checklist of bats in the study area and their abundance. The large number of cultivated trees such as mango and cashew nuts which produce fruits targeted by fruit bats also may have contributed to high abundance of frugivorous bats in the farmlands. Even though the farmlands around ASF were highly disturbed, bats were still found in them and the presence of orchards seems to benefit some bat species; hence, this study highlights the need to intensify more bat research in agricultural landscapes in Africa, in order to understand their role in the conservation of bats in the continent. Farmland biodiversity is greatly enhanced by the presence of trees (Lumsden and Bennett 2005, Fischer et al. 2010). Thus, there is a need to work with the local farmers in our study area, and encourage them to maintain the habitat heterogeneity of their farms – coupling the cultivation of annual plants with other permanent cultures, usually orchards – in order to continue to provide suitable foraging and roosting sites for bats, while supporting the production of fruits which are consumed locally or are sold to supplement household incomes.

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